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Review

Bovine noroviruses: A missing component of calf diarrhoea diagnosis

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ABSTRACT

Noroviruses are RNA viruses that belong to the Genus *Norovirus*, Family *Caliciviridae*, and infect human beings and several animal species, including cattle. Bovine norovirus infections have been detected in cattle of a range of different ages throughout the world. Currently there is no suitable cell culture system for these viruses and information on their pathogenesis is limited. Molecular and serological tests have been developed, but are complicated by the high genetic and antigenic diversity of bovine noroviruses. Bovine noroviruses can be detected frequently in faecal samples of diarrhoeic calves, either alone or in association with other common enteric pathogens, suggesting a role for these viruses in the aetiology of calf enteritis.

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Introduction

Morbidity and mortality due to calf diarrhoea are responsible for substantial economic losses in the cattle industry throughout the world (Virtala et al., 1996). Noroviruses (NoVs) are RNA viruses that belong to the Genus *Norovirus*, Family *Caliciviridae*, and have emerged as important causes of acute, non-bacterial, food and waterborne gastroenteritis in human beings worldwide (Patel et al., 2009). The prototype NoV, Norwalk virus, was first described by Kapikian et al. (1972). Through the use of electron microscopy (EM), viruses with typical calicivirus morphology have been identified in faecal samples of domestic animals (Scipioni et al., 2008b), including in faecal samples from diarrhoeic calves (Woode and Bridger, 1978).

The first bovine enteric caliciviruses (BoCVs), morphologically indistinguishable from human noroviruses (HuNoVs), were described in cattle in England (Bo/Newbury2/76/UK virus; Woode and Bridger, 1978) and Germany (Bo/Jena/80/DE virus; Günther et al., 1984; Günther and Otto, 1987). Subsequently, bovine noroviruses (BoNoVs) have been identified in America (Smiley et al., 2003; Wise et al., 2004), Africa (Hassine-Zaafrane et al., 2012) and Asia (Park et al., 2007). BoNoVs may play a role in the aetiology of calf enteritis (Scipioni et al., 2008b), but are not included in routine diagnostic algorithms for calf enteric diseases and their impact on livestock production remains unclear. The aim of this review is to describe these poorly known bovine enteric pathogens, to discuss their pathogenesis, to summarise available techniques for their diagnosis and to report their current molecular epidemiological features.

Genome organisation and molecular virology of noroviruses

The *Caliciviridae* family includes five genera (*Norovirus*, *Sapovirus*, *Lagovirus*, *Vesivirus* and *Nebovirus*) (Green, 2013), along with incompletely characterised, unassigned caliciviruses (Farkas et al., 2008; L'Homme et al., 2009; Carstens, 2010) (Fig. 1). The BoNoV genome is a single-stranded, positive sense, polyadenylated, 7.3–7.5 kbase RNA molecule (Liu et al., 1999; Oliver et al., 2007a). In the HuNoV genome, the 5′ end of the genomic RNA is covalently linked to the genome-linked viral protein (VPg) (Jiang et al., 1993). The untranslated regions (UTRs) at the 5′ end of all NoV genomes are typically 5–78 nucleotides (Green, 2013).

NoV genomes are organised into three open reading frames (ORFs), with the exception of murine norovirus (MuNoV), which has a fourth ORF (ORF4) (McFadden et al., 2011) (Fig. 2). Starting from the 5′ end of the genome, ORF1 encodes the viral non-structural proteins, ORF2 encodes the major capsid protein (VP1), and ORF3 encodes the minor structural protein (VP2). In the MuNoV genome, ORF4 produces virulence factor 1 (VF1), which regulates the innate immune response (McFadden et al., 2011).

Open reading frame 1 is translated as a large polyprotein of 1740 amino acids (aa), which is cleaved by the viral protease (3CLPro) to encode six mature non-structural (NS) proteins (Thorne and Goodfellow, 2014). The coding sequences for the N-terminal non-structural protein NS1-2 (p48), NS3 nucleotide triphosphatase (NTPase)/RNA helicase, NS4 protein (p22), NS5 protein (VPg), NS6 protease (3CLPro) and NS7 RNA-dependent RNA-polymerase (RdRp) are transcribed from the 5′ end to the 3′ end of ORF1, respectively.

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Fig. 1. Phylogenetic relationships between different human and animal, positive sense, single stranded RNA viruses, including bovine noroviruses highlighted in bold face in the tree. The tree was inferred with the maximum likelihood method on complete genomic sequences from representative viruses (see Appendix: Supplementary Table S1 for GenBank accession numbers), with 1000 bootstraps and the General Time Reversible + γ substitution model (Tamura et al., 2013).

ORF2 is translated as a 55–60 kDa protein, VP1, which is involved in self-assembly and capsid formation, receptor recognition, host specificity, strain antigenic diversity and immunogenicity (Chen et al., 2004). X-ray crystallographic structure studies using Norwalk virus-like particles (VLPs) showed that VP1 contains two major domains, a well-conserved shell (S) domain, which forms the core of the particle, and a more variable protruding (P) domain, which extends away from the central core (Prasad, 1999). The P domain is further divided into the P1 and the highly variable P2 subdomains (Fig. 3); the latter is involved in interaction with the host cell membrane (Tan et al., 2004; Tan and Jiang, 2014) and possesses the most important epitopes (Lindesmith et al., 2013). VP2 most likely is involved in capsid assembly and genome encapsidation (Vongpunsawad et al., 2013).

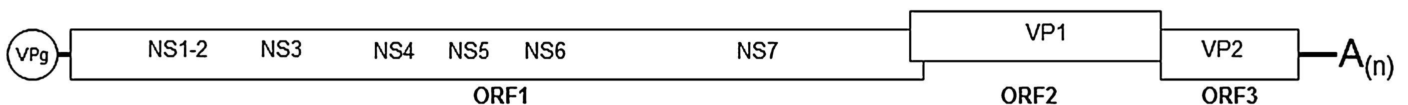
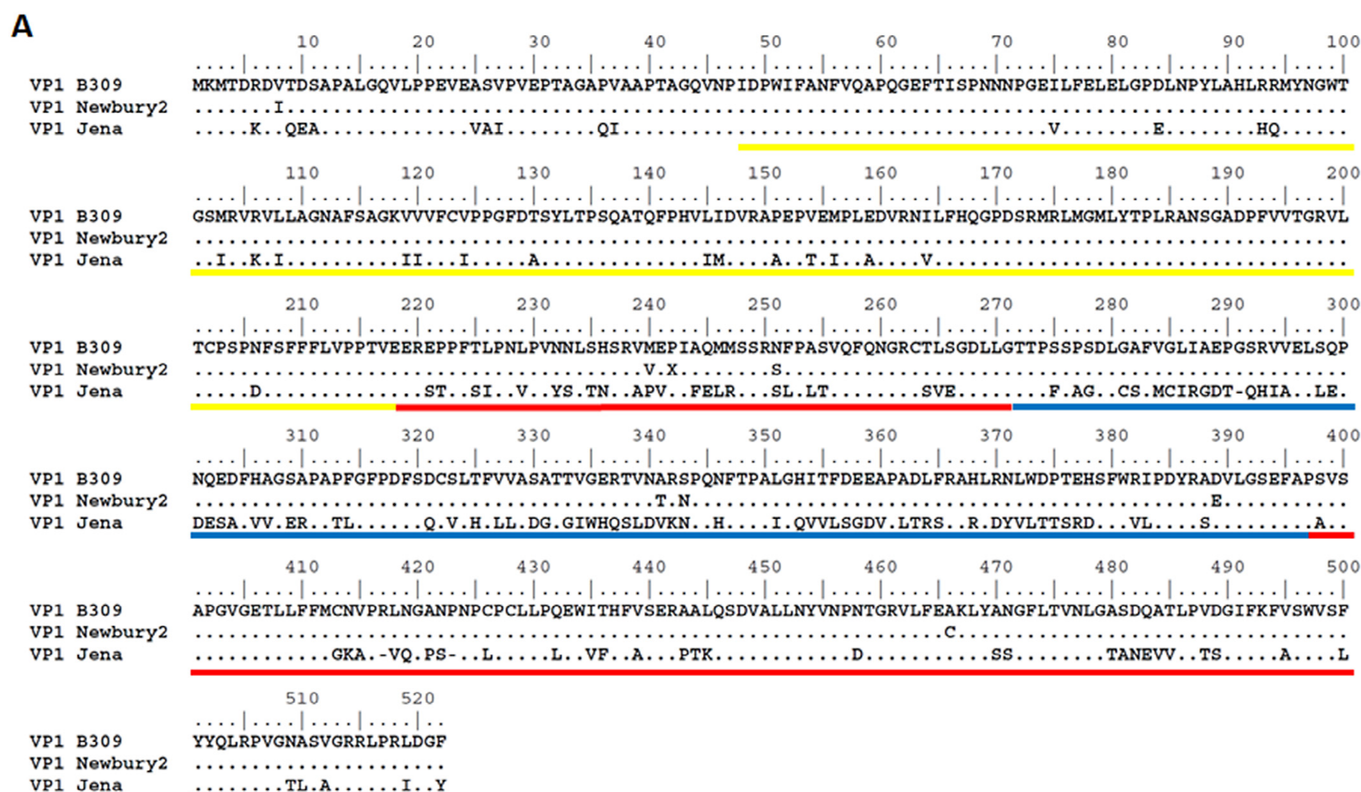


Fig. 2. Representative genomic organisation of the bovine norovirus genome.



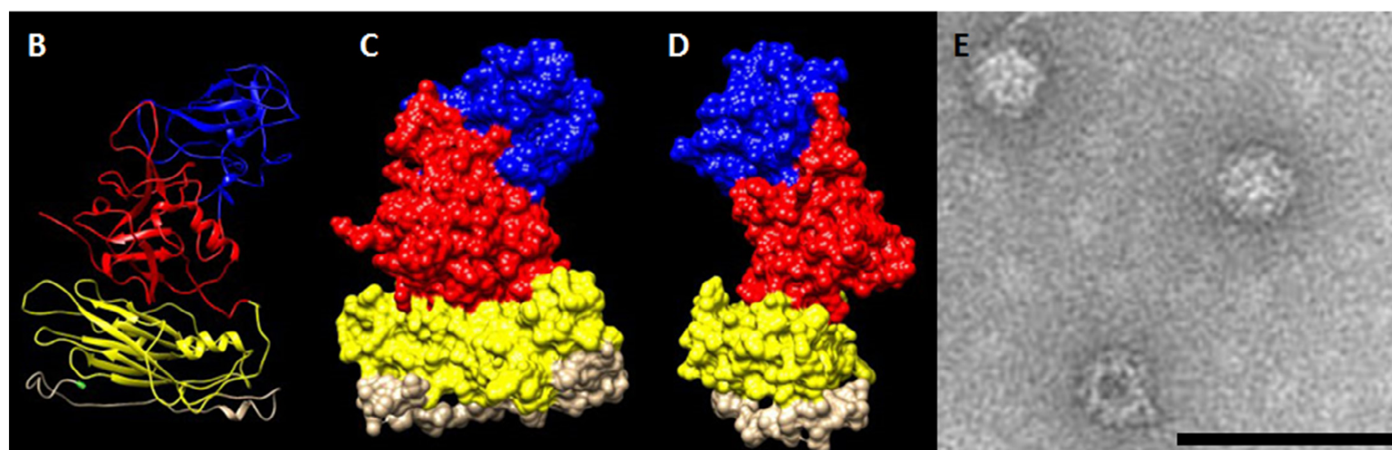


Fig. 3. (A) Multiple alignment between amino acid sequences of the two bovine norovirus reference strains, Jena (genotype 1) and Newbury 2 (genotype 2), and the B309 strain (identified in Belgium in 2003, Mauroy et al., 2012). The different domains of the proteins are identified in different colours in the sequence (yellow, S domain; red, P1 subdomain; blue, P2 subdomain). (B) Ribbon representation and (C, D) three-dimensional modelling of the bovine norovirus B309 amino acid sequence. The three-dimensional modelling was inferred with the Chimera software from the crystal structure of the Norwalk virus capsid protein. (E) Electron micrograph after uranyl acetate staining of B309 virus like particles. Scale bar = 100 nm.

Receptors for animal NoVs are not well characterised, but a role for carbohydrates related to histo-blood group antigens (HBGAs) as receptors or co-receptors has been demonstrated for HuNoVs (Tan and Jiang, 2014). Studies using recombinant VLPs have demonstrated that a Newbury2-related strain of BoNoV attaches to bovine duodenal epithelium through recognition of the αGal epitope, which is related to HBGAs, but absent in human and porcine tissues (Zakhour et al., 2009). Sialic acid has also been proposed as a minor or alternative receptor for Newbury2-related BoNoVs (Mauroy et al., 2011).

Classification of noroviruses

On the basis of phylogenetic relationships inferred from full length VP1 aa sequences, NoVs have been divided into six genogroups (GI to GVI) and multiple genotypes (Zheng et al., 2006; Martella et al., 2009). Genogroups I, II and IV infect humans and GII strains account for most human infections (Green, 2013). Noroviruses detected in animals have been classified as GII (pigs), GIII (ruminants), GIV (lions, cats and dogs), GV (mice) and GVI (dogs) (Woode and Bridger, 1978; Saif et al., 1980; Karst et al., 2003; Martella et al., 2007, 2008; Mesquita et al., 2010; Pinto et al., 2012). A third group of canine NoVs identified in dog faecal samples in Hong Kong (Tse et al., 2012) has been proposed as a new candidate genogroup (GVII) (Vinjé, 2015).

Comparisons of genomic sequences from the two original BoNoVs (Woode and Bridger, 1978; Günther et al., 1984; Günther and Otto, 1987) identified two genotypes within GIII, represented by the prototype strains Bo/Jena/80/DE and Bo/Newbury2/76/UK for genotypes 1 and 2, respectively (Liu et al., 1999; Oliver et al., 2003, 2007a).

Although NoVs are classified into genogroups and genotypes on the basis of the aa diversity in the complete VP1 sequence, recombination at the ORF1/ORF2 junction region is common. Consequently, a dual nomenclature system has been proposed, taking into account phylogenetic relationships of both partial RdRp (P) and capsid coding sequences (Kroneman et al., 2013). On the basis of this novel nomenclature system, the GIII.1 prototype strain Bo/Jena/80/DE is designated GIII/Bo/DE/1980/GIII.P1_GIII.1/Jena and the GIII.2 prototype strain Bo/Newbury2/76/UK is designated GIII/Bo/UK/1976/GIII.P2_GIII.2/Newbury2. Few BoNoV strains have been sequenced in full and few entire ORF2 sequences are available (Mauroy et al., 2012), which means that it has not been possible to establish robust phylogenetic relationships or rates of evolution of BoNoVs.

Recombination of noroviruses

Noroviruses have high genetic variability (Boon et al., 2011; Mauroy et al., 2014) and are able to undergo recombination (Bull et al., 2007). Phylogenetic divergences, as a consequence of recombination events between strains from different clusters, have been reported for sequences from human isolates for the polymerase and capsid coding regions (Bull et al., 2007). A copy choice mechanism has been proposed to explain recombination events in NoVs; most recombination events occur at the ORF1/ORF2 junction (Han et al., 2004; Bull et al., 2005, 2007), which is where the end of the RdRp gene and the beginning of the capsid protein gene are located. Another recombination breakpoint was proposed to exist at the ORF2/ORF3 junction in HuNoVs (Eden et al., 2013).

Due to the current genetic classification within the genus *Norovirus* and the main location of recombination events, the recombinant strain will cluster with different genotypes, depending on the phylogenetic origin of either its RdRp or capsid protein genes. To date, the detection of recombinant NoVs is based mainly on in silico methods (Oliver et al., 2004; Bull et al., 2007; Mauroy et al., 2009b; Di Martino et al., 2014a), but which could overestimate the occurrence of these events. In vitro recombination has been observed following co-infection of two parental MuNoV strains in a mouse leukaemic monocyte-macrophage cell line (RAW 264.7) (Mathijs et al., 2010).

Molecular studies have revealed the circulation of two recombinant BoNoV types, GIII.P1/GIII.2 and GIII.P2/GIII.1, with recombination breakpoints 16–19 nucleotides located upstream of the start of the ORF1/ORF2 junction (Bull et al., 2007). The first recombinant BoNoV strain, Bo/Thirsk10/00/UK, was identified in the UK by Oliver et al. (2004). This strain had a GIII.1-related RdRp sequence and a GIII.2-related capsid coding sequence. Molecular investigations from diverse geographical settings have revealed the circulation of a number of recombinant strains genetically related to Bo/Thirsk10/00/UK (Han et al., 2004; Mauroy et al., 2009b; Jor et al., 2010; Di Martino et al., 2014a). In contrast, only one strain, B-1SVD/03/US, was identified with a GIII.2-related RdRp and a GIII.1-related capsid coding sequence (Bull et al., 2007) (Fig. 4).

Pathogenesis and clinical features of bovine norovirus infections

The pathogenesis of BoNoVs is not well understood, but assumptions can be made from their comparison with HuNoVs. Human NoVs are highly infectious (Teunis et al., 2008) and are transmitted primarily by the faecal–oral route, from person to person, by contaminated food or water (Graham et al., 1994; Mathijs et al., 2012).

Diarrhoea is the most important clinical presentation in cattle infected with BoNoVs; on the basis of experimental studies, transient anorexia and a malabsorption syndrome have also been associated with BoNoV infection (Woode and Bridger, 1978; Günther and Otto, 1987; Otto et al., 2011; Jung et al., 2014). Diarrhoea can last for 3–4 days, being more severe in 3-week old animals than in neonatal calves (Günther and Otto, 1987).

Gnotobiotic calves infected with the GIII.1 BoNoV strain Bo/Jena/80/DE exhibited anorexia and diarrhoea, associated with necrosis of the intestinal epithelium and villous atrophy (Otto et al., 2011). In colostrum deprived immunocompetent calves, infection with Bo/Jena/80/DE induced diarrhoea for 2–3 days after inoculation (Otto et al., 2011). Inoculation of 4–7 day old gnotobiotic calves with the GIII.2 BoNoV strain CV186-OH/00/US induced acute diarrhoea, prolonged faecal shedding (median 28 days) and seroconversion, but no significant intestinal lesions (Jung et al., 2014).

BoNoVs have been detected using molecular methods in faecal samples of diarrhoeic calves, either alone or as co-infections with other enteric viruses, such as rotavirus, nebovirus, coronavirus and bovine viral diarrhoea virus (BVDV) (Smiley et al., 2003; Park et al., 2007; Mauroy et al., 2009a; Jor et al., 2010; Di Bartolo et al., 2011; Cho et al., 2013). It is possible that mixed infections influence the severity of BoNoV infections.

Inapparent infections have been reported in calves in The Netherlands and Italy (van der Poel et al., 2003; Di Martino et al., 2014a). In 272 faecal samples from 190 herds in Norway, GIII BoNoVs were detected using quantitative reverse transcriptase (RT)-PCR (qPCR) with almost equal prevalence in healthy (50.3%) and diarrhoeic calves (49.3%) (Jor et al., 2010). In a case–control study of calf diarrhoea in the USA, BoNoVs were identified by qPCR at higher frequency and at higher quantities in diarrhoeic calves than healthy calves (Cho et al., 2013). There is a need to conduct further studies in calves and adult cattle to determine the age-related susceptibility of cattle to BoNoVs.

Detection of bovine norovirus

Electron microscopy

The first diagnostic method for NoVs was electron microscopy (EM) (Doane, 1994), but this technique has low sensitivity, with a detection limit of ~10^6 viral particles/mL faeces (Atmar and Estes, 2001). The sensitivity of detection can be increased by immunoelectron microscopy (IEM) (Kapikian et al., 1972), but is still insufficient for routine diagnosis.

Molecular techniques

RT-PCR has been used to improve the sensitivity of detection of NoVs in faeces (Atmar and Estes, 2001). De Leon et al. (1992) developed an RT-PCR to detect viruses genetically related to Norwalk virus. Since then, several RT-PCR formats have been developed and have become the principal means for diagnosis of BoNoV infections (Wolf et al., 2007; Scipioni et al., 2008a, b and c). Most RT-PCR oligonucleotide primers have been designed to amplify the highly conserved region of the end of the RdRp gene, the start of the ORF2 gene and the NTPase/RNA helicase (NS3) coding sequence (Atmar and Estes, 2001; Table 1). Complete genomes have also been determined using a combination of different primer sets (Dastjerdi et al., 1999; Oliver et al., 2007a; Mauroy et al., 2012).

Novel molecular techniques have been developed for the diagnosis of HuNoV infections, with improved sensitivity and specificity (Notomi et al., 2000; Moore, 2004; Fukuda et al., 2006; Liu et al., 2009). Binding RT-PCR can be used to distinguish between infectious and non-infectious particles (Tian et al., 2010; Li et al., 2011). These methods can be also used to evaluate the genome integrity by combining binding RT-PCR with long-range RT-PCR (Li et al., 2011, 2014). These methods hold promise for application to diagnosis of BoNoV infections.

Antigen ELISAs

When expressed by baculovirus, capsid proteins of NoVs self-assemble into VLPs, which are morphologically and antigenically

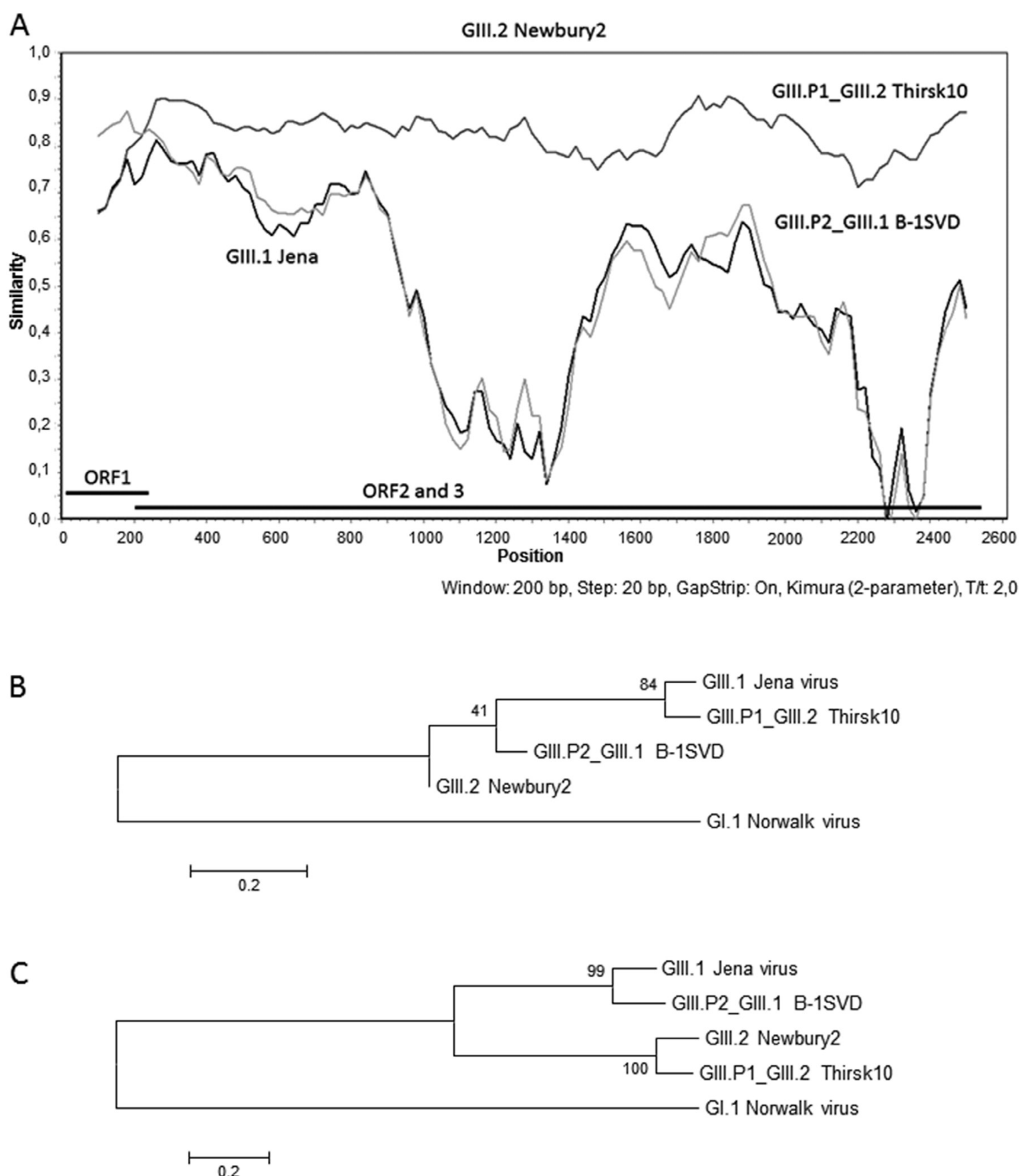


Fig. 4. Recombinant bovine noroviruses. (A) Simplot analysis of the two bovine norovirus reference strains (Jena virus and Newbury2 virus for genotypes 1 and 2, respectively) with the two prototype recombinant bovine noroviruses (Thirsk10 for GIII.P1_GIII.2 recombinant sequences and B-1SVD for GIII.P2_GIII.1 recombinant sequences). Percentages of similarity were measured along the partial RNA dependent RNA polymerase coding sequence (open reading frame 1, ORF1), the capsid protein coding sequence (ORF2) and the minor structural protein coding sequence (ORF3). Newbury2 virus was selected as the query sequence. (B) Phylogenetic relationships between bovine norovirus reference viruses and recombinant reference sequences in their polymerase coding region. The tree was inferred with the maximum likelihood method with 1000 bootstraps and the Kimura2 + γ substitution model. (C) Phylogenetic relationships between bovine norovirus reference viruses and recombinant reference sequences in their capsid protein coding region. The tree was inferred with the maximum likelihood method with 1000 bootstraps and the Hasegawa-Kishino-Yano + γ substitution model.

similar to infectious viral particles (Jiang et al., 1992; Green et al., 1993; Belliot et al., 2001; Han et al., 2005). VLPs are a source of antigens that can be used in serological assays (Jiang et al., 2000; Mauroy et al., 2009a; Di Martino et al., 2014b) and to produce polyclonal or monoclonal antibodies for antigen (Ag) ELISAs (Jiang et al., 2000; Han et al., 2005; Oliver et al., 2006). Ag ELISAs for detection of HuNoVs were less sensitive and specific than RT-PCR or qPCR (Rabenau et al., 2003; Kele et al., 2011), but may have value for low cost, high throughput screening of multiple faecal samples for HuNoVs; samples from suspected cases that are negative in the Ag ELISA should be retested by molecular methods. A BoNoV Ag ELISA was developed by Deng et al. (2003) for detection of BoNoV Bo/Jena/80/DE virus (GIII.1)-related capsid antigens in faecal samples of diarrhoeic calves.

Antibody ELISAs

Different assay formats for antibody (Ab) ELISAs have been used to assess the seroprevalence of NoVs in human beings and veterinary

Table 1
Comprehensive summary on different primers used in the literature for the molecular diagnosis of bovine norovirus infections.

Primer	Sequence (5′–3′)	Location[a]	Polarity	Annealing temperature (°C)	Target virus	References
BEC-POL5′	TATGAGCCAGCCTACCTTGG	3670-3689	+	45	NoV GIII.2	Smiley et al. (2003)
BEC-POL3′	ACCTGGGACGTGCATGGGA	4473-4454	–			
Jenacap-R1	AGTGGAAATTGCCGCCGATACAGC	6636-6659	–	50	NoV GIII.1	Han et al. (2004)
Jenacap-R2	GCATCCTCTCATCATGTTGG	6725-6744	–			
Jenacap-R3	AATTGCCGCCGATACAG	6637-6653	–			
NAcap-F	TCCTTCCCGATTTTGTAA	5044-5062	+	50	NoV GIII.2	Han et al. (2004)
NAcap-R	AACCCCGCCGAGAAGAGAGGAGAA	6659-6636	–			
Jenacap-F1	TGATTTGTCGCTGTGGGAAGGT	5001-5022	+	54	NoV GIII.1	Han et al. (2004)
Jenacap-F2	AGCGGCGGAATGGAGAT	4939-4955	+	50		
CCV1	CAAAGGTCAAAGAGCAATCGGA	6042-6020	–	NS	NoV GIII.2	van der Poel et al. (2003)
CCV2	CTCAGTTCAATTTCAAAACGGC	5824-5846	+			
CCV3	GGCTTTCCAGATTTTTCCGATTG	6005-6028	+	60	NoV GIII.2	van der Poel et al. (2003)
CCV4	GGCACGCTCGGAAACAAAATG	6392-6371	–			
CBECU-F	AGTTAYTTTTCCTTYTAYGGBA	4555-4577	+	55	NoV GIII.2	Smiley et al. (2003)
CBECU-R	AGTGTCTCTGTCAGTCATCTTCAT	5087-5063	–			
CBECU-INTF	GTCGACGGYCTKGTSTTCCT	4702-4722	+	NS	NoV GIII.2	Park et al. (2006)
CBECU-INTR	CACAGCGACAAATCATGAAA	5028-5008	–			
J11U	CCATCAACCATTGGATTTTGAC	4477-4499	+	50	NoV GIII.2	H. Tsunemitsu[b]
J11L	ACCTGGCGGCGAAGCTCAATTG	4703-4681	–			
J21U	AACCATTGGATATTAACCCTGTG	4482-4505	+	54	NoV GIII.2	H. Tsunemitsu[b]
J21L	GACCATCTACCTGCTGCTTCA	3473-3452	–			
Calfpol1	TTCCTGCTGGCAGTGCACG	4417-4436	+	NS	NoV GIII.2	van der Poel et al. (2003)
Calfpol2	CAGAGGTCACCAACTTGGAC	4514-4534	+			
JenaORF3	CAGTGGTAAACGATCTGTATT	7245-7224	–	NS	NoV GIII.2	Reuter et al. (2009)
Z5pol-R	GGAGGACTTGGCCAAGGG	5121-5103	–			

NS, not specified.
[a] Primer sequences are mapped to the genomic sequence of BoNoV strains Bo/Jena/80/DE (GenBank AJ011099) and Bo/Newbury2/1976/UK (GenBank AF097917) for GIII.1- and for GIII.2-related sequences, respectively.
[b] Primer sequences based on bovine enteric caliciviruses (BEC) identified in Japanese dairy calves genetically related to BEC/Jena and NA-2 were kindly shared by Hiroshi Tsunemitsu, Japanese National Institute of Health-Scichinohe Research Unit, Shichinohe, Aomori, Japan.

species (Jiang et al., 2000; Deng et al., 2003; Farkas et al., 2005; Di Martino et al., 2010). Ab ELISAs have been developed to screen bovine serum samples using GIII.1 or GIII.2 BoNoV VLPs expressed in the baculovirus system (Deng et al., 2003; Oliver et al., 2007b; Mauroy et al., 2009a; Thomas et al., 2014). Ab ELISAs are more broadly reactive than Ag ELISAs and heterologous responses among genetically closely related strains can be difficult to differentiate. Therefore, antibodies detected by such Ab ELISAs cannot be interpreted as a response to infection with a particular strain.

Distribution of bovine noroviruses

GIII.2 strains of BoNoVs are the most prevalent worldwide (Table 2; Fig. 5). In Europe, the molecular prevalence of GIII.2 ranges from 1.8% to 50.3% (van der Poel et al., 2003; Ike et al., 2007; Mijovski et al., 2010). In The Netherlands, 31.6% of pooled faecal samples from veal calf farms and 4.2% of individual faecal samples from dairy cattle were positive for GIII.2 BoNoVs by RT-PCR (van der Poel et al., 2003). In the UK, BoNoVs were detected by RT-PCR in 11% of diarrhoeic samples (Milnes et al., 2007). In Belgium, 7.5% of faecal samples from diarrhoeic calves ranging in age from 1 week to 6 months were positive for GIII.2 BoNoVs and 93.2% of serum samples collected from calves and adult cattle contained IgG antibodies against GIII.2 BoNoVs (Mauroy et al., 2009a). In Italy, GIII.2 BoNoVs have been detected by RT-PCR in 7.9% of diarrhoeic cattle in mixed infections with rotaviruses (Di Bartolo et al., 2011) and in 8.6% of clinically healthy calves (Di Martino et al., 2014a).

In the USA, the prevalence of GIII.2 BoNoVs by RT-PCR was 72% in veal calves in Ohio (Smiley et al., 2003), 80% in calves with diarrhoea in Michigan and 25% in calves with diarrhoea in Wisconsin (Wise et al., 2004). A high prevalence (94–100%) of IgG antibodies against GIII.2 BoNoVs has been detected in cattle in New Mexico, Arkansas and Ohio (Thomas et al., 2014). In contrast, BoNoVs were detected in 1.6% of bovine faecal samples in Canada (Mattison et al., 2007).

In South Korea, 9.3% of 645 faecal samples were positive for BoNoVs by nested RT-PCR, of which 5.9% of samples also tested positive for other enteric pathogens, including bovine coronavirus, BVDV, bovine torovirus, rotavirus, nebovirus and *Escherichia coli* (Park et al., 2007). Of 12 South Korean BoNoV sequences determined in this study, 11 had the highest nucleotide (88.0–90.5%) and amino acid (93.5–99.1%) similarities with GIII.2 strains, while one sequence was genetically related to GIII.1. In Africa, BoNoVs were detected in 16.6% of diarrhoeic calves in Tunisia (Hassine-Zaafrane et al., 2012). In South America, BoNoVs were detected in 1.0% of cattle in Venezuela (Alcalà et al., 2003).

GIII.1 BoNoVs are detected less frequently, suggesting that these viruses constitute a minor cluster. Reported frequencies of GIII.1 BoNoVs in Europe include 1/47 (2.1%) in Hungary (Reuter et al., 2009), 1/300 (0.3%) in Belgium (Mauroy et al., 2009b), 3/101 (2.9%) (Di Bartolo et al., 2011) and 1/104 (0.9%) (Di Martino et al., 2014a) in Italy and 25/456 (5%) in France (Kaplon et al., 2011) (Table 2).

In the USA, GIII.1 BoNoV sequences were detected in 5/74 (6.8%) dairy calves with diarrhoea in Michigan and Wisconsin (Wise et al., 2004). IgG antibodies against GIII.1 BoNoV were detected in 99.1% of cattle in Germany (Deng et al., 2003). In the same study, GIII.1 BoNoVs were detected in 8.9% of faecal samples using an Ag ELISA (Deng et al., 2003).

Molecular investigations in several countries have revealed a number of potential recombinant strains, most of them genetically related to the prototype strain Bo/Thirsk10/00/UK (Oliver et al., 2004). Sequence analysis of the ORF1/ORF2 region demonstrated recombinant type GIII.P1/GIII.2 in Belgium (Mauroy et al., 2009b), Norway (Jor et al., 2010) and Italy (Di Martino et al., 2014a). In the USA, Han et al. (2004) identified the recombinant GIII.P1/GIII.2 strain CV521-OH/02/US in Ohio. In a study of NoV recombinants from all genogroups worldwide, Bull et al. (2007) identified a recombinant strain (B-1SVD/03/US) with a GIII.2 polymerase and a GIII.1 capsid (GIII.P2/GIII.1) sequence. The growing detection rate of recombinant Bo/Thirsk10/00/UK-like (GIII.P1/GIII.2) sequences highlights the

Table 2
Overview of bovine noroviruses detected worldwide (adapted from Mathijs et al., 2012).

Continent	Country	Period	Number of herds	Herd type	Age (days)	Type of samples	Samples (n)	Positive samples	Age of positive animals	Norovirus genotype	Reference
Europe	Belgium	2002–2003	NS	Dairy-Beef	NS	Individual	29	14	NS	ND	Scipioni et al. (2008c)
		2007			7–180		133 (D)	10 (7.5%)		GIII.2	Mauroy et al. (2009a)
		2008		NS	NS		300 (D)	28 (9.3%)	Calves and young stock	GIII.P1_GIII.2 GIII.2	Mauroy et al. (2009b)
	France	NS	NS	NS	NS	Individual	136 (NS)	25 (18.4%)	NS	GIII	Zakhour et al. (2010)
		12/2005–09/2008	415		9 (Mean)		456	89	NS	GIII.1 and GIII.2	Kaplon et al. (2011)
	Germany	1999–2002	147	Dairy	7–28	Individual	381 (D)	34 (8.9%)	NS	ND	Deng et al. (2003)
		05–06/2003	29	NS	All ages		41 (D)	2 (4.9%)	Calves	GIII.2	Ike et al. (2007)
	Hungary	02/2002	2	NS	1–2700	Individual	47 (NS)	4 (8.5%)	<9 days (1) 6–7 months (3)	GIII.1 GIII.2	Reuter et al. (2009)
		02/2008	NS		>20		26 (NS)	1 (3.8%)	Calves	GIII.2	
	Italy	2004–2005	NS	NS	7–20	Individual	101 (NS)	3 8	NS	GIII.1 GIII.2	Di Bartolo et al. (2011)
		11/2011–7/2012	16		0–42	Individual	104	1 (0.9%) 9 (8.7%) 1 (0.9%)		GIII.1 GIII.2 GIII.P1_GIII.2	Di Martino et al. (2014a)
	The Netherlands	1997–1999	NS	Veal-Beef	7–365	Pooled	243 (NS)	77 (31.6%)	NS	GIII.2	van der Poel et al. (2003)
		1999–2000		Dairy	1–730	Individual	312 (D + N)	13 (4.2%)	1–9 months		
		1998	75	Veal-Beef	7–365	Pooled	120 (N)	25 (20.8%)	NS		van der Poel et al. (2000)
			45	Dairy	1460–2190			0			
	Norway	06/2004–12/2006	190	Dairy (126) Veal (64)	<90 (385) <90 (34)	Individual	419 (D + N)	209 (49.6%)	Calves (mean 42 days)	GIII.2 GIII.P1_GIII.2	Jor et al. (2010)
	Slovenia	2004–2005	4	NS	120–150	Individual	119	2 (1.9%)	Calves	GIII.2	Mijovski et al. (2010)
	United Kingdom	1998–2000	NS	NS	NS	Individual	476 (D)	38 (8.0%)	<6 weeks 4 months 2 cows	GIII.2	Oliver et al. (2003)
		1998–2000		Dairy (35%) Beef (65%)	All ages		398 (98% D)	44 (11.1%)	NS	ND	Milnes et al. (2007)
America	Canada	05–10/2006	45	Dairy	NS	Pooled	179 (NS)	3 (1.6%)	NS	GIII.2 GII.4-like	Mattison et al. (2007)
	United States	06–07/2000	4	Veal Beef	1–42	Pooled Individual	358 (NS)	258 (72.1%)	NS	GIII.1 and GIII.2	Smiley et al. (2003)
		03–04/2002									
		NS	8	Dairy	5–10	Individual	60 (D)	48 (80%)	Neonatal calves	GIII.2	Wise et al. (2004)
			14	Dairy	NS		14 (NS)	4 (28.6%)	NS		
		2002	4	Veal Beef	15		25 (NS)	14 1	NS	GIII.2 GIII.P1_GIII.2	Han et al. (2004)
		1999–2001	NS	Feedlot	180–210		103 100 140	103 (100%) 99 (99%) 132 (94%)		GIII.2	Thomas et al. (2014)
				Veal calves	7–10		47	47 (47%)			
	Venezuela	1994–2000	NS	NS	NS	Individual	129 (NS)	1 (0.9%)	NS	GIII	Alcalà et al. (2003)
Asia	South Korea	2004–2005	629	Veal-Beef	2–90	Individual	645 (D)	18 (2.8%) 60 (9.3%)	Calves	GIII.1 GIII.2	Park et al. (2007)
	Turkey	NS	NS	NS	1–60	Individual	70 (D)	6 (8.5%)	Calves	GIII.2	Yilmaz et al. (2011)
Africa	Tunisia	1/2006–10/2010	17	Dairy-Beef	NS	Individual	169 (D)	28	NS	GIII.2	Hassine-Zaafrane et al. (2012)
Oceania	New Zealand	05/2006	2	NS	<365 up to >730	Individual	28 (N)	15 (5.6%)	Calves, young stock and cows	GIII.1	Wolf et al. (2007)

NS, not specified; ND, not determined; N, non-diarrhoeic; D, diarrhoeic.

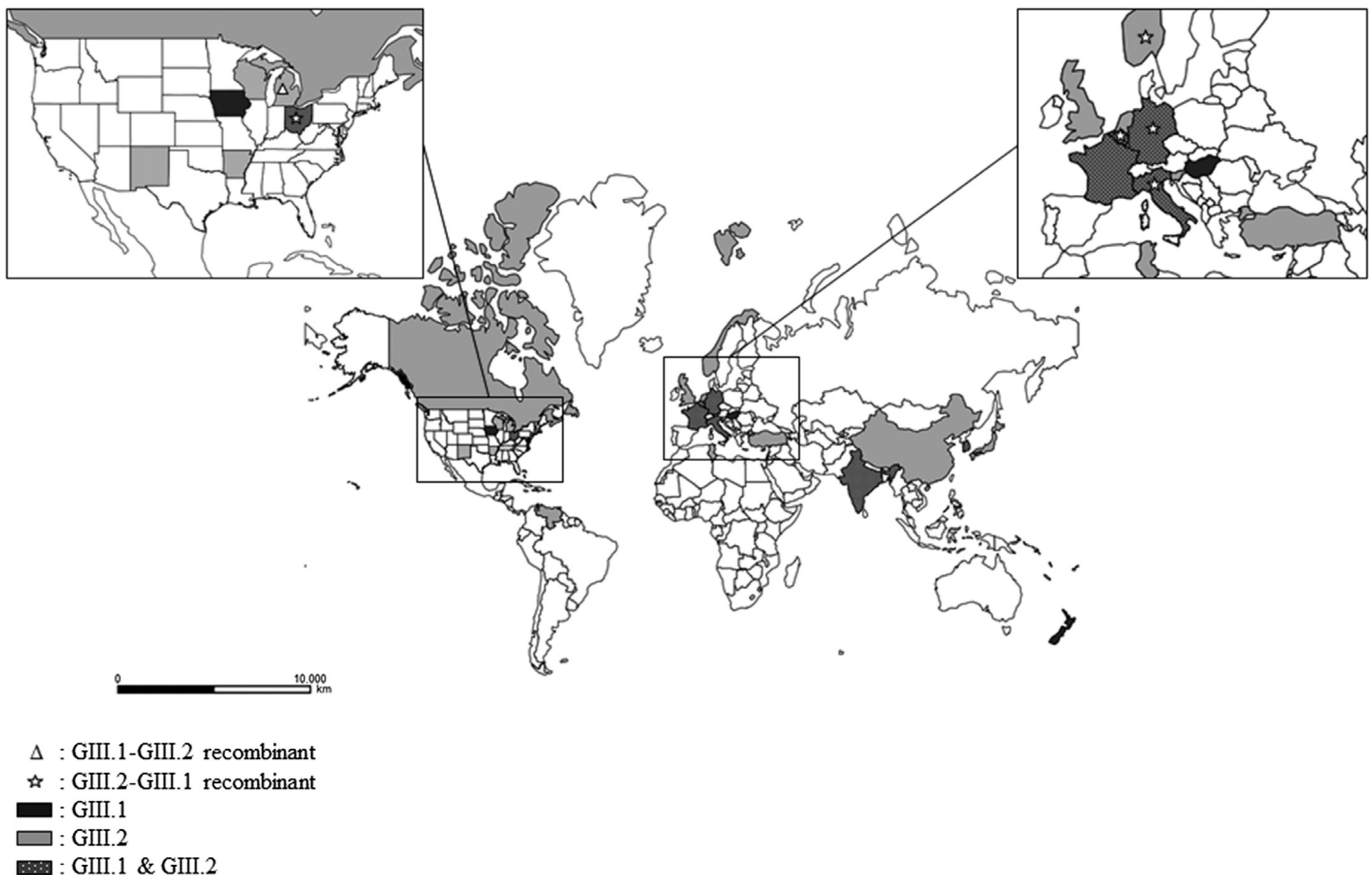


Fig. 5. Worldwide distribution based on available data of the bovine norovirus genotypes. The figure was created using the Quantum GIS software (http://qgis.osgeo.org) based on the molecular characterisation of the bovine norovirus isolates performed in the course of different studies. Detailed information around the original data is reported in Table 2.

need to consider these strains when detecting BoNoV and raises interesting questions about how these viruses emerge in an underlying context of low circulation of GIII.1 viruses.

Conclusions

NoVs are important enteric pathogens in children and vaccines have been developed to prevent human infections. NoVs have also been detected in cattle throughout the world and their role as enteric pathogens has been demonstrated in calves. BoNoVs should be considered in the differential diagnosis of calf diarrhoea and are candidates for inclusion in future vaccines in cattle.

Conflict of interest statement

None of the authors of this paper have a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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Appendix: Supplementary material

Supplementary data to this article can be found online at doi:10.1016/j.tvjl.2015.10.026.

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